



Reproductive Ecology of *Vallisneria americana* Michaux

by Dwilette G. McFarland

BACKGROUND: Commonly known as wild celery, *Vallisneria americana* Michaux (Figure 1) is an important component of aquatic plant communities in central and eastern North America. Established stands provide food and habitat for a variety of invertebrates, sport fish, and waterfowl—most notably the canvasback, *Aythya valisneria* (Wilson) whose species name was derived from the scientific name of the plant (Haller 1974, Poe et al. 1986, Korschgen et al. 1988). Abundant growth of *V. americana* can help to consolidate loose sediments, take up nutrients that support nuisance growth of algae, oxygenate the water, and improve water quality and clarity (Smart et al. 1994, Rogers et al. 1995, Wigand et al. 2000).

Declines in submersed aquatic vegetation (SAV), including *V. americana*, have been widely reported since the 1960s, especially from the Upper Mississippi River to the Chesapeake Bay region (Fischer and Claflin 1995, Moore et al. 2004). These losses in SAV have prompted considerable research to identify causal conditions and to develop effective restoration methods. Reasons for the declines remain uncertain, but most appear to be linked to serious natural and/or anthropogenic disturbances, e.g., eutrophication, drought, flooding, herbicides, navigation, and herbivory (Cooke 1983, Kemp et al. 1983, Carter and Rybicki 1985, Twilley et al. 1985, Kimber 1994, Kimber and Barko 1994, Rogers et al. 1995, Stewart et al. 1997). Thus far, attempts to restore *V. americana* have not all been successful because requirements for propagule growth in the field were not adequately met. Developing effective restoration strategies for SAV requires thorough knowledge of species biological traits and propagule production, early stages of growth, and establishment in response to key environmental factors (e.g., light, temperature, and sediment and water chemistry).

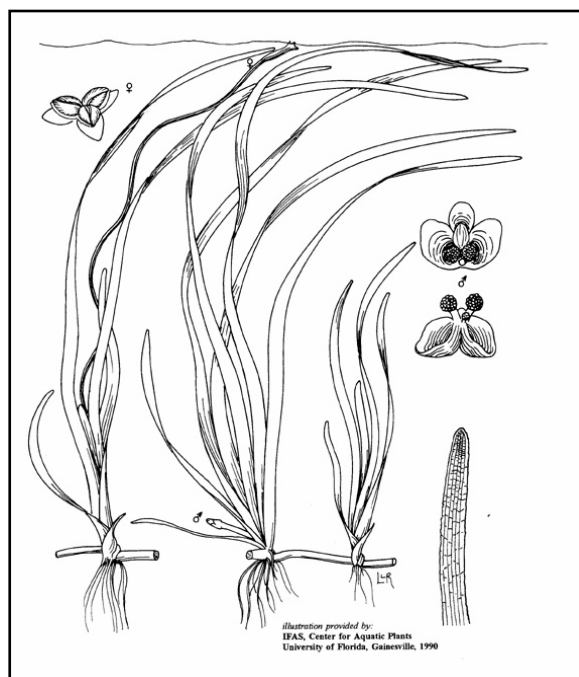


Figure 1. *Vallisneria americana* Michx. Image by IFAS, Center for Aquatic Plants, Univ. of Florida, Gainesville, 1990

PURPOSE: Nearly 20 years have passed since Korschgen and Green's publication (1988) on the ecology of *V. americana*, as a guide for restoration programs. While their report provides a wealth of important information, a great deal of research has been generated since their review was conducted. This technical note presents an update on the reproductive ecology of

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V. americana, based on available literature, much of which was published over the last two decades.

SPECIES PROFILE:

Taxonomy. *Vallisneria* is one of 17 genera of the frog-bit (Hydrocharitaceae) family, which consists of a large, diverse group of monocotyledonous, mostly perennial, aquatic herbs. Fifteen genera (including *Vallisneria*) occur primarily in fresh to brackish waters, while the remaining two genera occur mainly in marine environments (Cowardin et al. 1979, Flora of North America (FNA) 2004, Watson and Dallwitz 2005, Germplasm Resources Information Network (GRIN) 2005).

Identification of *Vallisneria* species has historically been problematic due to plastic responses to changes in the environment and similarities among taxa in floral morphology. The present consensus is that the genus consists of two separate species, and that each species, in turn, is differentiated into two varieties: 1) *V. spiralis* L. var. *spiralis* is found in Europe and southwest Asia, and 2) *V. spiralis* var. *denseserrulata* Makino, in Africa, Asia, Oceania and Australia; 3) *V. americana* Michaux var. *americana*, is found in the Americas, East and Southeast Asia, Oceania, and Australia, and 4) *V. americana* var. *biwaensis* (Miki) Lowden, comb. nov. in Japan, Hispaniola, and Venezuela. These taxa are delineated based on floral distinctions described by Lowden (1982) in his taxonomic treatment of the genus.

Misidentification of field specimens of *Vallisneria* has resulted in numerous synonyms for *V. americana* in published literature. The North American plant (*V. americana* var. *americana*) originally described by Michaux (1803) has been reported by many others as a variety of the European species *Vallisneria spiralis* (Gray 1848, 1874; Chapman 1883; Britton and Brown 1913). Adding further confusion to the nomenclature, populations of large, robust plants were named *Vallisneria neotropicalis* Marie-Victorin denoting the region of natural occurrence (Marie-Victorin 1943, Long and Lakela 1971). Godfrey and Wooten (1979) expressed concern about the distinctness of this species, suggesting that large plants may result in southern climates from conditions favoring growth over a longer growing season. This is likely the case for plants growing in clearwater springs in Florida, where year round, the springs remain at a nearly constant cool temperature (~ 21 °C). Lowden (1982) has provided an extensive list of synonyms for *V. americana* (var. *americana*), which at the species level includes: *V. neotropicalis*, *V. spiralis*, *V. gigantea*, *V. asiatica*, *V. subulispatha*, *V. higoensis*, and *V. natans*. Though widely known as wild celery, *V. americana* var. *americana* is also called water celery, American wildcelery, eelgrass, tape grass, canvasback grass, duck celery, oxtongue, plantain, and flumine-Mississippi (McAtee 1939; GRIN 2005; U.S. Department of Agriculture, Natural Resources Conservation Service (USDA NRCS) Plants National Database 2005). For simplicity, *V. americana* or wild celery will be used to indicate *Vallisneria americana* var. *americana* throughout this manuscript.

Distribution. *V. americana* is native to eastern North America and is common from southern Canada southward to Texas and Florida. The northern part of its range extends east in Canada from Nova Scotia, west through southern Quebec and northern Ontario to southeastern Manitoba (Catling et al. 1994). Though absent from Saskatchewan and Alberta, it occurs in southern British Columbia including two known locations on Vancouver Island (Catling et al. 1994). In the United States, this species is listed in 40 states (Figure 2), with recent reports from the west in

the states of Washington, New Mexico, and Arizona (USDA NCRS Plants National Database 2005). It has been documented as the most abundant SAV species in the Lake Huron-Lake Erie Corridor (comprised of the St. Clair River, Lake St. Clair, and Detroit River) (Schloesser et al. 1985; Schloesser and Manny 1986, 1990). It has been found south of the United States in Mexico, Cuba, Guatemala and Honduras, and probably because of its broad synonymy, is also reported from east and southeast Asia, Oceania and Australia (Lowden 1982, Korschgen and Green 1988).

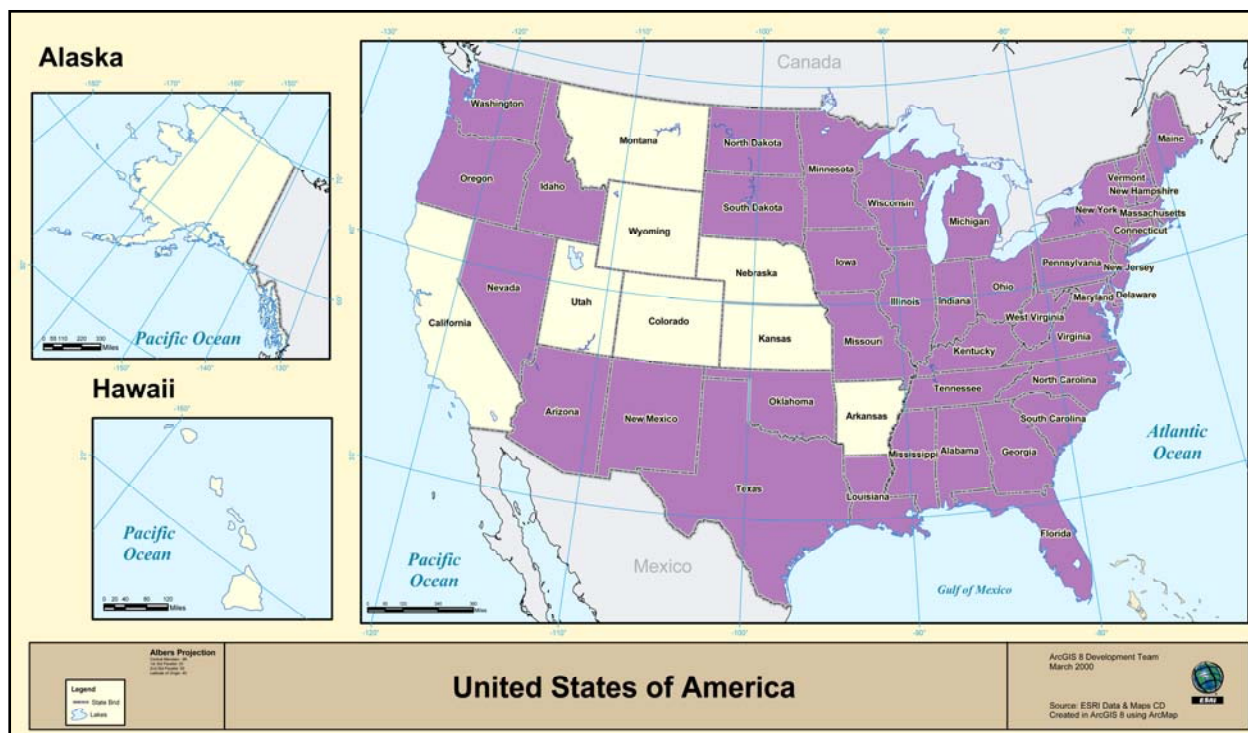


Figure 2. Distribution of *Vallisneria americana* Michx. in the United States. Lavender-shaded states indicate species presence, according to USDA NCRS Plants National Database, 2005

Morphology and Reproduction. Wild celery is a perennial, submersed aquatic plant, with ribbon-like leaves, up to 2 m or more in length, depending on water movement and depth (Lovett-Doust and LaPorte 1991). The leaves arise in a cluster (rosette) from a short vertical stem that sends out rhizomes and stolons from which new shoots develop (Figures 3 and 4). Leaves are finely veined and show a central longitudinal stripe (Figure 3). Roots are unbranched and fibrous at the base of each rosette. Leaf tips are bluntly rounded; leaf margins entire to conspicuously toothed (Figure 5).

According to Lowden (1982), two variants exist in the United States:

- **Narrow-leaved variant**—with leaves less than 10 mm wide, from 3 to 5 longitudinal veins, and margins entire to finely toothed; blades with perceivable to invisible transverse pigmented striations; found in freshwater inland waterways, lakes and lagoons.

- **Broad-leaved variant**—with leaves 10 to 25 mm wide, from 5 to 9 veins, and conspicuously toothed margins; blades with many visible transverse pigmented striations; found in coastal freshwater inlets or spring-fed waterways with nearly constant year-round temperatures, subject to brackish water inputs at high tide. [Catling et al. (1994) noted this variant does not occur in Canada.]

Individual plants of *V. americana* are either male or female (dioecious) and are capable of reproducing through asexual (vegetative) and sexual means. Pollination of female flowers takes place at the water surface (epihydrophily) and is adapted to avoid pollen hydration before transport onto receptive stigmata (Wylie 1917, Svedelius 1932, Kausik 1939, Hill 1965, Cox 1988). Flowering usually occurs in mid to late summer; fruits mature by early fall (Catling et al. 1994). Pistillate flowers (Figure 6) have three sepals and three white petals and are borne singly in a tubular spathe (a large bract or modified leaf) on a peduncle (stalk) that elongates upward. As many as 2000 staminate flowers, each approximately 0.6 mm in diameter, fit tightly into an ovoid spathe on a short peduncle attached near the base of the plant (Wylie 1917) (Figure 7). An abscission zone develops on this short peduncle, allowing the spathe to float and release its staminate flowers on the surface. Surface-tension depressions formed by pistillate flowers force staminate flowers to slip downward and tip pollen grains onto the stigmata. During submersion by waves, pistillate flowers may also form bubbles that enclose flowers of both sexes together, enabling flower tumbling and transfer of pollen (Svedelius 1932; Cox 1988, 1993).

After pollination, the stalk of the pistillate flower begins to coil, drawing the fruit downward where it continues to develop under water. The fruits are cylindrical capsules (Figure 8), 5 to 15 cm in length, each with hundreds of tiny, dark seeds (1.8 to 2.6 mm long x 0.6 to 1.0 mm wide) embedded in a mass of clear to whitish gelatinous material. In field populations, each capsule may contain approximately 150 to 500 seeds with viability as high as 93 to 98 percent (Godfrey and Wooten 1979, Lovett-Doust and LaPorte 1991, Lokker et al. 1997).



Figure 3. Mature *V. americana* showing ribbon-like leaves and central stripe along their lengths. Photo from the Aquatic Plant Information System (APIS) CD-ROM version 2.0; U.S. Army Engineer Research and Development Center (ERDC), 2001



Figure 4. Rosettes along a stolon of *V. americana*. Photo by J. Kujawski, Maryland Plant Material Center, 1997

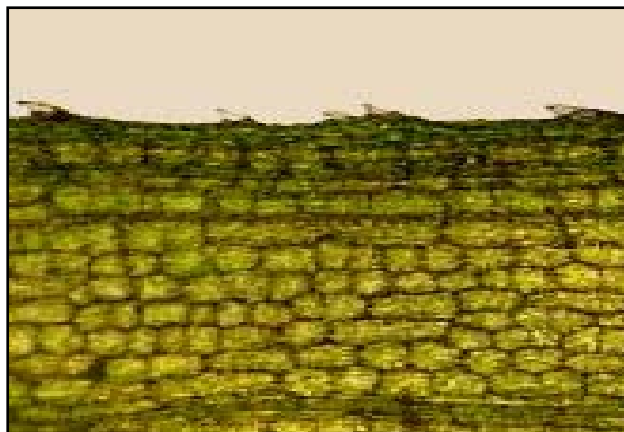


Figure 5. Leaf section of *V. americana*. Photo from the APIS CD-ROM, version 2.0; ERDC, 2001



Figure 6. Pistillate (female) flowers of *V. americana*. Photo by Maryland Department of Natural Resources (MDNR), 2005

An emphasis on clonal growth in *V. americana* is reflected by the production of a variety of asexual propagules. Winter buds (Figure 9) are produced in the sediments in cool temperate regions as a means of reestablishing the population after over-wintering; these propagules are also referred to in the literature as tubers and turions, though discrepancies concerning the distinctness of these structures are acknowledged by some experts (M. S. Ailstock 2006, pers. comm.). After lying dormant throughout the winter, the winter bud elongates in spring, sending a specialized stem (stolon) to the sediment-water interface from which a new plant emerges (Wilder 1974). In a single growing season, this new plant may generate 20 to 40 ramets (Korschgen and Green 1988, Catling et al. 1994) along rhizomes and stolons, serving to expand the population laterally over short distances. Because vegetative propagules of *V. americana* are normally anchored or buried in sediment, they are less likely than seeds to be swept to new sites by water



Figure 7. Spathes containing staminate (male) flowers of *V. americana*. Photo by MDNR, 2005



Figure 8. Seeds and seed pods of *V. americana*. Photo by ERDC, 2000



Figure 9. Winter buds of *V. americana*. Photo by the MDNR, 2005

movements or wind. Thus, for *V. americana*, seeds provide a potentially important mechanism for dispersal while also serving to establish new genotypes from existing populations.

The production of winter buds for carbohydrate storage and over-winter survival has been well documented for *V. americana* naturalized in northern climates (Korschgen and Green 1988, and literature therein). However, basal stem sections and root stocks may play a similar role as winter buds for the perennation of *V. americana* in the South, although this has been less frequently reported (Haller 1974). These observed differences in plant phenology have led to the recognition of different U.S. ecotypes (northern versus southern; as per Smart and Dorman (1993), Smart et al. (2005)) with possible genetic and other distinctions that need to be investigated. To the author's knowledge, no records of winter buds exist for *V. americana* field populations in tropical or sub-tropical locations. Interestingly, Godfrey and Wooten (1979) make no mention of these buds in *V. americana* in southeastern states, and Haller (1974) reported none in year-round harvests of the species from ponds in south-central Florida. Clark and Stout (1995), who studied reproductive phenology of *V. americana* in Mobile Bay, Alabama, found seeds but no winter buds of the species in sediment cores throughout the year. The lack of winter buds in the southern ecotype could be an inherent characteristic (Dawes and Lawrence 1989, Smart and Dorman 1993). Recent studies at the Lewisville Aquatic Ecosystem Research Facility, in Lewisville, Texas, showed that winter buds were produced only by the northern ecotype when the two ecotypes were tested under the same environmental conditions (R. M. Smart 2005, pers. comm.).

REPRODUCTIVE RESPONSE TO ENVIRONMENTAL FACTORS: The abundance of SAV, including *V. americana*, may vary over time for many reasons. Principal factors that interact in influencing plant morphology and production of biomass may also directly or indirectly impact plant reproductive capacity. Abiotic factors (e.g., light, temperature, and sediment nutrients) have received much investigative attention to determine their role in SAV growth and propagule development. Biotic factors (e.g., herbivory and disease) can also exert important influences on SAV dynamics but, to date, they have been less rigorously studied than abiotic factors. Presented below is information on *V. americana*, with reference to the production, dispersal, and growth of different types of propagules. The first section deals with factors influencing sexual reproduction, and the second section, factors affecting asexual reproduction. Because of increased interest in the use of seed in site restoration projects, some of the most recent quantitative work has centered on factors influencing growth through sexual reproduction. Summary tables are provided to outline reproductive responses of *V. americana* to factors as addressed by cited references (Tables 1-6).

SEXUAL REPRODUCTION: Literature on the reproduction of SAV indicates that these populations are maintained primarily through asexual means and that contributions from seeds are often minimal (Sculthorpe 1967, Kautsky 1990). Yet, many species of SAV, despite their dominant clonal nature, have retained the ability to flower and produce large numbers of viable seeds. A major advantage of sexual reproduction is genetic variation, which increases the chance of surviving dramatic environmental change, e.g., disease, drought, flooding, drawdown, and herbicide treatment (Williams 1975, Galinato and van der Valk 1986, Watkinson and Powell 1993). Seeds may also play a key role in dispersal and colonizing new areas (Kimber et al. 1995a, McFarland and Rogers 1998) and thus may be important in shaping SAV population structure, distribution, and resilience.

V. americana has long been known to produce viable seeds (Muenscher 1936) but information on seedling establishment in situ is very limited. Kimber et al. (1995a) reported that following a drought in the late 1980s, sites in the Upper Mississippi River were apparently re-colonized by seeds of *V. americana*. The seedlings produced winter buds after only one season of growth and were observed in areas where *V. americana* had not previously grown. Other establishments of *V. americana* seedlings have been observed in Ostego Lake, New York (Titus and Hoover 1991) and in populations of the southern ecotype at Toledo Bend Reservoir on the Texas-Louisiana border (Smart and Dorman 1993, Kimber et al. 1995a). These reports demonstrate that *V. americana* can become established from seed notwithstanding a formidable array of possible limitations on the growth of young seedlings in situ.

For SAV in general seed production is potentially difficult because it is multifaceted by nature and may be interrupted at many points in the process. As identified by Titus and Hoover (1991), seed production may be inhibited by factors that restrict: 1) flowering—including floral induction, floral initiation, morphogenesis and anthesis; 2) pollen transport and deposition onto receptive stigmas; 3) pollen tube germination and development; 4) fertilization; and 5) embryogenesis and fruit maturation. Among these, they suggested the hardest steps for SAV to achieve are the production of flowers and transport of pollen to receptive stigmas (cf. Titus and Hoover 1991 for further discussion). Though self-incompatibility and seed abortion (Stephenson 1981, Barrett 1988) are challenges that should not be overlooked (Titus and Hoover 1991), there is presently too little information on these processes for meaningful synthesis.

Flowering and Pollen Transport. *V. americana* typically flowers only once a year, from late June to September (Table 1) under long (>13-hr) photoperiod and moderate to high (> 20 °C) temperature (Donnermeyer 1982, Titus and Stephens 1983, Best and Boyd 2001). Its summer-flowering habit may be related to changes in plant nutrition, in that only in summer, when days are long and warm, is there sufficient plant biomass for flowers to develop (Grainger 1947, Sculthorpe 1967, Weiner 1988, Waller 1988). Because it flowers during summer, it is classified as a long-day plant (Salisbury and Ross 1985) but the critical day length to prompt flowering in this species has not been determined.

Titus and Hoover (1991) examined the role of plant biomass (on a dry weight basis) in determining the incidence of flowering in *V. americana* in greenhouse studies (Table 1). They reported that the percentage of plants flowering rose linearly from 7 percent for plants weighing less than 0.5 g to 100 percent for all plants ($n = 148$) above 2.0 g dry weight. Of 425 plants, 88 percent followed a 0.75-g threshold rule: plants weighing less than 0.75 g failed to flower, and those weighing more than 0.75 g produced flowers. The ratio of female flower number to plant biomass (mean = 1.47 flowers g^{-1} , $n = 33$) was significantly lower than the ratio of male inflorescence number to plant biomass (mean = 2.87 inflorescences g^{-1} , $n = 94$). Coefficients of variation for these ratios were generally quite high (50 percent and 54 percent, respectively), reflecting a high level of uncertainty even in a semi-controlled (greenhouse) environment.

Water depth may pose an obstacle to pollination of *V. americana* by limiting the ability of pistillate flowers to float on the water surface (Table 1). In surveys of Nuthatch Hollow Pond, all subsurface flowers failed to develop fruit, although fruit set was 92 percent among surfacing flowers (Sullivan and Titus 1996). In Seneca Lake, which harbors abundant *V. americana* in relatively deep water, female plants flowered across the depth range of the population (from 2.25

to 5.25 m), though their flowers were unable to reach the surface and consequently were not pollinated (Sullivan and Titus 1996). Additional studies at Silver Lake showed that increases in water depth, from 0.9 to 2.5 m, decreased the percentage of surfacing female flowers of *V. americana*: nearly all female flowers surfaced from plants at 0.9 to 1.3 m, with only 6 percent surfacing at 1.7 m, and none at 2.1 to 2.5 m (Sullivan and Titus 1996).

Table 1			
Flowering and pollen transport in beds of <i>V. americana</i> in relation to abiotic (a) and biotic (b) factors			
Factor/Type	Plant Response	Ecotype and Location	Reference
Flowering (Occurrence)			
Photoperiod (a)	Late Jul through Aug; long photoperiod	Northern; Lake Mendota, WI	Titus & Adams 1979
	Late Jun to early Aug; long photoperiod	Northern; a lake in WI	Witmer 1937
	Early Jul to early Sep; long (decreasing) photoperiod	Northern; Potomac River, MD	Carter & Rybicki 1985
	Jul to mid-Sep; long photoperiod	Northern; Lake Huron-Lake Erie corridor (south Ontario)	Catling et al. 1994
	Early Jun to Sep; peak Jul to Aug; long photoperiod	Northern; Pamlico River Estuary, NC	Zamuda 1976
	Mid Jul thru Aug; long photoperiod	Northern; Chenango Lake, NY	Titus & Stephens 1983
Plant Biomass (b)	Plants weighing < 0.75 g (dry) fail to produce flowers; > 2.0 g optimal	Northern; greenhouse facility	Titus & Hoover 1991
Temperature (a)	May be affected indirectly through impacts on biomass; paucity of information on direct temperature effects	Nonspecific; based on observations of SAV in general	Grainger 1947; Sculthorpe 1967
Pollen Transport			
Water Depth (a)	Though flowering occurred over a range from 0.9 to 2.5 m, sub-surface flowers at 2.1 to 2.5 m failed to be pollinated	Northern; Silver Lake, PA	Sullivan & Titus 1996
	Sub-surface flowering occurred in a deepwater population at 2.25 to 5.25 m; no evidence of pollination	Northern; Seneca Lake, NY	Sullivan & Titus 1996
Water Movement (a)	Increases in surface velocity negatively affect pollination; velocities > 0.3 m s ⁻¹ can prevent pollination	Northern; Hudson River, NY	Sullivan & Titus 1996
	Pollination increased in sites protected from waves and wind as compared with open-water locations	Northern; Cayuga Lake, NY	Sullivan & Titus 1996

Pollination of *V. americana* may be limited by wind, waves, and surface currents carrying male flowers away from a site before female flowers are pollinated (Table 1). Sullivan and Titus (1996) reported that fruit set in Cayuga Lake decreased to 79 percent at unprotected, open-water sites exposed to wind and waves; this contrasted greatly with fruit set that occurred in protected areas (97 percent) where leaves and female flowers along the surface hindered dispersal of male flowers. They also observed high levels of fruit set (100 percent) in female plants at Silver Lake, where an enclosure was used to confine male flowers to increase their residence time in the vicinity of female plants. These researchers speculated that short residence time of male flowers might be offset by high densities of male flowers to increase the chance of pollination.

Fruit set in *V. americana* growing in the Hudson River was found to correlate negatively with surface velocity, and was reduced to zero at velocities greater than 0.3 m s⁻¹ (Sullivan and Titus 1996; Table 1). Pollen transfer was greatly hindered because male flowers were floating past the

anchored female flowers, and because female flowers became oriented downstream, positioning them away from incoming male flowers. Moreover, damage to the female perianth and female flowers being driven below the water surface were noted to reduce the potential for pollination in high-velocity ($> 0.3 \text{ m s}^{-1}$) waters.

Dormancy and Germination. Innate dormancy has been described as an inability of the seed to germinate even in the presence of suitable external conditions (Harper 1977). Germination of innately dormant seeds often requires some special condition(s) to be satisfied, such as photoperiod, light intensity, abrasion (scarification) of the seed coat or cold stratification (Ferasol et al. 1995). This type of dormancy is interpreted to introduce a temporal delay in germination that provides additional time for seed dispersal over greater geographical distances. It also offers a possible means of maximizing seedling survival by resisting germination until conditions for seedling growth become more conducive. In temperate climates, seeds normally germinate after adverse conditions of winter when the seedling is more likely to experience favorable growth conditions during the spring (Salisbury and Ross 1985).

For seeds of *V. americana*, pre-chilling enhances germination, but is not an absolute requirement for seeds to germinate (Table 2). This was demonstrated in studies by Ferasol et al. (1995) where some fruits of *V. americana* were stored (moist) at 4 °C and others at 20 °C for 75 days. Following storage, the seeds were placed in Petri dishes and allowed to germinate under a 13-hr photoperiod at approximately 12 °C. (The photoperiod-temperature regime that was selected for this study was to emulate early spring conditions experienced by in situ sediments in a temperate climate.) For the first 40 days after storage, untreated seeds germinated more rapidly than seeds that had undergone the prescribed cold stratification; but by the end of 100 days, compared to untreated seeds, the germination percentage was significantly higher for cold-stratified seeds.

Early work by Muenscher (1936) demonstrated that seeds of *V. americana* could be stored at 1 to 3 °C for many months and remain capable of germinating soon after planting or removal from cold storage (Table 2). In his studies, 71 percent of untreated seeds germinated within 2 months in a greenhouse at temperatures of 18 to 21 °C during the day and 13 to 16 °C at night. Germination percentages remained high at 76, 87, and 82 percent for seeds that had been cold stored just above freezing (at 1 to 3 °C) in the dark for 2, 5, or 7 months, respectively.

Testa color and structure have been found to correlate significantly with the maturity and germinability of seeds of *V. americana* (Table 2). Ferasol et al. (1995) reported that seed coats of mature *V. americana* seeds are rough and brown, compared to the smooth, white seed coats of the immature seeds. The rough surface of mature seeds is due to the many fenestrated tubercles that may help stabilize and anchor the seed once deposited onto a substrate. Compared to the mature seeds in their studies, immature seeds germinated more rapidly but germination percentage of mature seeds was significantly higher. Scarification of mature seeds significantly increased germination; up to 90 percent of scarified seeds germinated within 60 days, whereas fewer than 30 percent of non-scarified seeds germinated over the same period. In view of these findings, the authors proposed that the need for scarification may compensate for the lack of a strict cold pretreatment requirement. Germination may be delayed by the seed coat until after autumn and winter when more favorable conditions for seedling growth prevail.

Table 2 Seed dormancy and germination in <i>V. americana</i> in relation to abiotic (a) and biotic (b) factors		
Factor/Type	Seed Dormancy and Germination	Reference
Burial Depth (a)	Burial depths < 15mm optimal for germination	Campbell & Moore 2005
Desiccation (a)	Can kill seed embryos; no survival after 2 months of air-drying	Muenscher 1936
Dissolved Oxygen (a)	Germination increases under aerobic conditions ($DO > 4 \text{ mg l}^{-1}$)	Campbell & Moore 2005
Light (a)	Germination can occur in both light and dark conditions, but the latter significantly increases the number of seeds that germinate	Kimber et al. 1995a
	Germination is insensitive to light gradients at low levels (i.e., from 2 to 25 percent full sun over the growing season)	Kimber et al. 1995a
Salinity (a)	Germination increases significantly at salinities < 5 ‰	Campbell & Moore 2005
Scarification (a)	Seeds exhibit an innate physical dormancy; seed coat must be degraded for mature seed to germinate	Ferasol et al. 1995
Sediment Organic Matter Content (b)	Germination maximized in substrate with < 3 percent organic matter content	Campbell & Moore 2005
	Germination may be delayed on more organic sediments	Hoover 1984
Seed Age (b)	Compared to mature (brown) seeds, immature (white) seeds germinate more rapidly, but overall, show lower germination percentages	Ferasol et al. 1995
Temperature (a)	Cold stratification enhances germination but is not <i>required</i> for seeds to germinate	Ferasol et al. 1995
	Viability remains high in seeds after 7 months of storage in water at temperatures just above freezing (1 to 3 °C)	Muenscher 1936
	Over a range in temperature from 13 to 31 °C, germination increases significantly at temperatures > 19 °C	Campbell & Moore 2005

Seeds of *V. americana* can germinate in either light or dark, although the latter significantly increases percentage germination (Table 2). Kimber et al. (1995a) reported that over a range in light levels from 0 percent (dark) to 25 percent full sun (i.e., $228 \text{ mol m}^{-2} \text{ s}^{-1}$ at mid-day), 68 percent of the seeds germinated in the dark, while 30 to 48 percent germinated in the light treatments. Specific light levels did not affect percentage germination, indicating that the seeds may be insensitive to rather low light gradients. These findings are similar to those of Muenscher (1936) who showed that percentage germination of *V. americana* seeds was unaffected by light intensity; however, he noted that germination that occurred in direct sunlight was slower and less even among seeds than in diffuse sunlight.

The importance of seeds to recovery of declining populations of aquatic plants may lie in part in their ability to remain viable during severe disturbances such as drought or drawdown. Relatively high germination percentages after prolonged periods of drying (more than 3 months) have been demonstrated for seeds of some aquatic plants such as *Myriophyllum spicatum* (Standifer and Madsen 1997), and *Veronica anagallis-aquatica* and *Rorippa nasturtium-aquaticum* (Muenscher 1936). Conversely, *V. americana* seeds show no great resistance to desiccation as they failed to germinate after air-drying for 2 months under greenhouse conditions (Muenscher 1936; Table 2).

Current Studies on Seed Germination—Preliminary Findings. Recently, research was undertaken to address gaps in the literature concerning environmental influences on germination of *V. americana* seeds. The research was performed specifically to assess total percentage germination over selected ranges in light availability (present or absent), temperature (13 to

31 °C), sediment organic matter content (1 to 8 percent), burial depth (2 to 100 mm), salinity (0 to 15 ‰) and dissolved oxygen content (< 2 or > 4 mg l⁻¹). Initial results were presented in October 2005 at the Conference of the Estuarine Research Federation in Norfolk, Virginia (Campbell and Moore 2005). These studies indicate that germination in *V. americana* seeds increases significantly at temperatures greater than 19 °C, salinities less than 5 percent, organic matter content less than 3 percent, burial depths less than 15 mm, and when oxygen is present (greater than 4 mg l⁻¹) (Table 2). The presence or absence of light apparently had no significant effect on germination—a response differing slightly from the results of Kimber et al. (1995a) probably owing to differences in experimental methods.

Dispersal. Among primary modes of dispersal, including water, animals (including man) and wind, water is perhaps the most important in disseminating aquatic plant species that have naturally buoyant fruits and seeds (Sculthorpe 1967). Though seeds of *V. americana* are negatively buoyant, its fruits, depending on physical condition, may float for several days before falling onto the sediment (Wilder 1974; Kaul 1978; Clark and Stout 1995; McFarland, pers. obs., Table 3). A short period of flotation could be sufficient to allow transport to sites well away from the competitive habitat of established parent vegetation (Sculthorpe 1967). In contrast, a well-ripened fruit that has become waterlogged may sink fairly quickly, distributing its contents within or in the vicinity of the parent plant bed (Kaul 1978). Seedbank studies in Lake Onalaska found that densities of seeds of *V. americana* were greater within or somewhat downstream of an established bed than in upstream or open-water areas (McFarland and Rogers 1998). Maps of water movements in the lake revealed a prevailing southward flow that coincided with the southward drift and deposition of seeds relative to mature bed location.

Frequency of transport of *V. americana* seed by various mechanisms is unknown, but it is highly conceivable that animals, particularly wildfowl, provide both long- and short-range dissemination. For any SAV species, direct observations of this type of dispersal would be difficult, yet many researchers have provided circumstantial evidence for exo- and endozoic transport of SAV fruits, seeds, and other propagules (Sculthorpe 1967 and literature therein, Figuerola and Green 2002, Green et al. 2002, Santamaria 2002). The extent to which human activities (e.g., recreational boating, aquatic gardening, and aquarium trade), animals, water movements, and wind each account for the spread of *V. americana* propagules warrants further investigation.

Seedling Establishment. The morphology of germination and establishment of seedlings of *V. americana* has been documented in detail by Haccius (1952) and Kaul (1978). Their observations provide insight into the vulnerability of tiny seedlings in the initial stages of lodging on a substrate to the emergence of roots and the first plumular leaves. Beyond studies by these two authors, quantitative research on seedling establishment in *V. americana* in response to environmental conditions has been rather limited. Impacts of light on seedlings of this species have been examined in a few investigations, but information is lacking concerning effects of other factors (e.g., sediment instability, temperature, salinity, particle loads, and pathogens). Ranges of tolerance of young seedlings are probably much narrower than for mature vegetation and need to be quantified for *V. americana* seedlings.

Table 3 Seed dispersal and establishment of seedlings of <i>V. americana</i> in relation to abiotic (a) and biotic (b) factors		
Factor/Type	Seed/Seedling Function	Reference
Dispersal		
Buoyancy (b)	Seeds are negatively buoyant; fruits removed from the parent plant may float up to several days; well-ripened fruits sink more readily	Wilder 1974, Kaul 1978, Clark & Stout 1995, Kimber et al. 1995a
	Seed deposition greater within or downstream of established parent bed	McFarland & Rogers 1998
Establishment		
Light (a)	Seedlings survive and produce winter buds at light levels > 9 percent surface sun	Kimber et al. 1995a
	The relationship between light and seedling survival is a sigmoid curve: survival increases rapidly in the range of 0 to 5 E m ⁻² d ⁻¹ and is excellent at levels above 10 E m ⁻² d ⁻¹ ; levels below 3 E m ⁻² d ⁻¹ cause high mortality	Doyle & Smart 2001
pH (a)	Seeds exposed to low pH (< 6) produce significantly smaller plants that are less likely to reproduce, either sexually or asexually	Titus & Hoover 1993
Turbidity (a)	Over a range in turbidity from 0.2 to 45 NTU (53 to 7 percent total incident light), seedling survival, rosette production and biomass are progressively diminished	Doyle & Smart 2001

Kimber et al. (1995a) assessed light requirements of seedlings of *V. americana* based on seedling emergence and winter bud production under different light regimes. Sediments collected from Pool 8 (Lake Onalaska) of the Upper Mississippi River were incubated in outdoor ponds shaded over the growing season with fabric that reduced light to 2, 5, 9, and 25 percent full sun. Though seeds germinated at all light levels, survival and bud production were significantly enhanced in treatments with at least 9 percent of the surface light level (Table 3). This minimum requirement for growth of seedlings was the same as for plants from winter buds (Kimber 1994) and was similar to the 10-percent requirement for *V. americana* clonal reproduction, based on Potomac River studies (Carter and Rybicki 1990).

Doyle and Smart (2001) found that turbidity, due to effects on light availability, can strongly affect seedling growth in *V. americana*. Over a range in turbidity treatments from 0.2 to 45 NTU (53 to 7 percent total incident light), seedling survival, rosette production, and biomass were progressively diminished (Table 3). Calculations using their data along with that from Kimber et al. (1995a) revealed that the relationship between light and seedling survival is a sigmoid curve: survival increases rapidly between 0 and 5 E m⁻² d⁻¹ and is excellent at levels above 10 E m⁻² d⁻¹; mortality is high at levels below 3 E m⁻² d⁻¹.

Field surveys by numerous workers have reported *V. americana* in aquatic systems ranging in pH from 5.4 to 10.2 (Moyle 1945, Fassett 1957, Crowder et al. 1977, Crow and Helquist 1982, Korschgen and Green 1988). However, the few reports of this species occurring at pH 6 or less indicate that it may not grow well or persist in waters with low pH. Titus and Hoover (1993) found, in greenhouse studies where effects of pH were tested, that *V. americana* from seed at pH 5 produced no flowers and too few winter buds to replace themselves. Plants grown from seed at pH 5 were reduced by at least 90 percent in dry biomass compared to those grown from seed at pH 7.5 (Table 3).

ASEXUAL REPRODUCTION: For *V. americana*, as for many SAV species, asexual reproduction is the dominant means of population increase and over-wintering (Titus and Stephens 1983,

Titus and Hoover 1991, Philbrick and Les 1996). During the growing season, the plant spreads laterally through rhizomes and stolons (horizontal stems) that grow respectively below and above ground, generating new rosettes at the nodes. Its winter buds serve primarily for perennation and represent a physiological commitment to carbohydrate storage, and protection of meristematic tissues during adverse conditions; these propagules become independent of parent vegetation usually in winter when organs connecting them to the parent stop growing and deteriorate. Morphologies of different types of asexual propagules of *V. americana* have been described by Bellrose (1941), Wilder (1974), Donnermeyer (1982), Donnermeyer and Smart (1985) and Catling et al. (1994). Discussions below focus mainly on *V. americana* winter buds, since data specific to rhizomes and stolons are rare in ecological literature.

Propagule Induction. In northerly climates, winter buds form near the end of the growing season from late summer through autumn (Table 4), under decreasing temperature and shortening photoperiod (less than 14 hr, Best and Boyd 2001). These buds remain dormant in sediment throughout the winter and begin to sprout into young plants with warming temperatures of spring (Sculthorpe 1967, Hutchinson 1975, Grace 1993, van Vierssen 1993). Environmental induction of winter buds in certain SAV species (e.g., *Hydrilla verticillata*, *Potamogeton crispus*, *P. nodosus*, and *P. pectinatus*) has shown sensitivity to photoperiod, temperature, nutrients, quantum flux density and/or spectral quality (Sculthorpe 1967, Van et al. 1978, Klaine and Ward 1984, Spencer and Anderson 1987). Critical requirements of these factors if they exist for *V. americana* have not been investigated thoroughly under controlled conditions.

Table 4			
Production of winter buds of <i>V. americana</i> in relation abiotic (a) and biotic (b) factors			
Factor/Type	Winter Bud Formation	Ecotype and Location	Reference
Photoperiod (a)	Mid Aug through Oct; peaks in early Oct; decreasing (mostly short) day length	Northern; Pool 9, Upper Mississippi River	Donnermeyer & Smart 1985
	Late Aug through Sep; decreasing (mostly short) day length	Northern; Chenango Lake, NY	Titus & Stephens 1983
	Late summer through autumn; decreasing (mostly short) day length	Northern; Lakes Wingra and Mendota, WI	Titus & Adams 1979
	Mid Sep through Oct; decreasing (mostly short) day length	Northern; Lake Huron-Lake Erie corridor (south Ontario)	Catling et al. 1994
	None produced	Southern; Juniper Run, FL	Dawes & Lawrence 1989
	None produced	Southern; transplants to Lewisville from Toledo Bend, TX	Smart & Dorman 1993
Plant Biomass (b)	3.25 to 3.60 winter buds produced g ⁻¹ dry biomass, for plants initiated from winter buds; plant biomass (dry) and winter bud number closely correlated (r^2 from 0.82 to 0.92, $P < 0.01$)	Northern; greenhouse and field studies in NY	Titus & Hoover 1991 and literature cited therein
	Winter bud production is a high priority in plants grown from seed; plant biomass (dry) and winter bud number correlated well ($r^2 = 0.78$, $P < 0.01$)	Northern; greenhouse in NY	Hoover 1984

Titus and Hoover (1991) performed linear regressions using data from field and greenhouse studies to analyze the relationship between biomass of *V. americana* plants and the number of winter buds produced (Table 4). For plants grown from winter buds, the slopes ranged from 3.25 to 3.60 buds g⁻¹ dry biomass, and for plants grown from seed, a relatively high slope (14.92 buds

g⁻¹ dry biomass) was obtained. For both groups, the correlation between winter bud number and plant (dry) biomass was high: r^2 ranged from 0.8 to 0.9 for plants grown from winter buds and was 0.78 for plants grown from seed.

Sprouting and Emergence. Vertical profiles of the distribution of winter buds of *V. americana* in the Potomac River showed that the majority of these buds were buried 5 to 15 cm deep in sand and 10 to 20 cm deep in silty clay (Rybicki and Carter 1986). The ability of winter buds to emerge from deeper in the substrate is advantageous since deeper burial protects against desiccation and wildfowl grazing. Rybicki and Carter (1986) showed that winter bud emergence was lower in sand than in silty clay, and declined in both substrate types with increases in burial depth (Table 5). None of the buds survived at depths greater than 25 cm in either substrate and emergence from both substrates was 90 percent or more from a burial depth of 10 cm.

Table 5 Sprouting and emergence of winter buds of <i>V. americana</i> in relation to biotic (b) and abiotic (a) factors		
Factor/Type	Winter Bud Sprouting and Emergence	Reference
Burial Depth (a)	Winter bud emergence decreases with increases in burial depth; burial depths ≤ 10 cm appear optimal for emergence	Carter et al. 1985; Rybicki & Carter 1986
Morphology (b)	Winter buds formed in chains often show "first-formed bud dominance," where the second bud develops into a rosette only if the first bud germinates or is severed or clipped.	Titus & Hoover 1991; McFarland 1999, unpubl. data
Salinity (a)	Over a range in salinity from 0 to 15 ‰, germination negatively correlated with salinities ≥ 3 ‰	Carter & Rybicki 1987 (unpubl. data)
	Winter buds fail to germinate at salinities > 11 ‰	Carter & Rybicki 1987 (unpubl. data)
Sediment Type (a)	Percentage emergence of winter buds buried in sand is generally lower than for winter buds buried in fine-textured silty sediment	Rybicki & Carter 1986
Temperature (a)	Winter buds germinate when water temperatures reach 10 to 14 °C	Zamuda 1976; Rybicki & Carter 2002
	Germination maximized at temperatures near 20 °C	Rybicki & Carter 2002
	Timing of germination under field conditions can be predicted based on accumulation of heat units or degree-days	Spencer et al. 2000

The ability of *V. americana* to withstand periods of high salinity infusion may be important in determining its occurrence in tidally influenced estuaries. Studies by the U.S. Geological Survey examined germination of *V. americana* winter buds at salinities ranging from 0 to 15 ‰ (Carter and Rybicki 1987, unpubl. data, Table 5). The results showed that germination was little affected at 3 ‰ or less, but at 13 ‰ and greater, all of these propagules failed to germinate. At 3 ‰, germination was 80 percent, but declined to 7 percent at 11 ‰.

Winter buds of *V. americana* germinate in spring after over-wintering, when water temperatures reach 10 to 14 °C (Zamuda 1976; Rybicki and Carter 2002, Table 5). Accumulation of degree-days (also referred to as heat units) can now be used in a model to predict the timing of emergence of *V. americana* from winter buds established in nature (Spencer et al. 2000). Increases in water temperature from 13 to 22 °C increase the rate and percentage of winter bud germination (Rybicki and Carter 2002) but mechanisms of dormancy and pre-chilling requirements for germination have not been clearly established for these propagules.

Quite often, winter buds of *V. americana* are borne in pairs or even in triplets and show a sequential germination pattern with respect to bud position on the chain (Table 5). Titus and Hoover (1991) observed that after planting 20 double buds of this species, 19 rosettes subsequently developed but only from the first-formed bud on the chain. Their studies and those of others (McFarland, unpubl. data) show that the second-formed bud can form a rosette, but only if: 1) the first bud germinates or emerges, 2) its connection to the first rosette is severed, or 3) leaves from the first germinated bud are clipped.

Vegetative Establishment. Post-germination vigor and ability to survive in sub-optimal environments are plant characteristics that rely heavily on propagule size and nutritional reserves (Table 6). A large propagule, with abundant carbohydrate and mineral nutrient pools, appears more likely to establish a root system and emerge from greater depths in the substrate (cf. Spencer 1987; Titus and Hoover 1991). Titus and Hoover (1991) noted that winter buds of *V. americana* in Chenango Lake showed the greatest mortality (greater than 75 percent) in low freshweight classes of 0.5 g or less. In contrast, survival was greatest in larger winter buds, especially in the heaviest freshweight classes from 1.1 to 1.8 g. Size may also be a good predictor of competitive outcome since larger winter buds of *V. americana* produce larger rosettes, more new winter buds, and greater biomass (Hoover 1984, Korschgen et al. 1997, Titus and Hoover 1991, Doyle and Smart 2001).

While *V. americana* can initially elongate and develop from winter buds in the dark (Korschgen and Green 1988), subsequent growth and reproduction are negatively influenced by low levels of light (Table 6). Studies conducted in Lake Onalaska showed that transplants from winter buds grew well and produced replacement-weight winter buds in locations where irradiance was at least 9 percent full sun (Kimber et al. 1995b). These findings were supported by pond investigations where, over a range in light (from 2 to 25 percent surface irradiance), *V. americana* from winter buds produced replacement-weight winter buds in 9 percent light or greater. Extending the growing period tended to compensate for impacts of low light: plants grown at 5 percent full sun also produced winter buds but only when the growth period was sufficiently lengthened (Kimber et al. 1995b).

Similar to their findings concerning growth of *V. americana* from seeds, Doyle and Smart (2001) reported that growth from winter buds was adversely influenced by increases in turbidity (Table 6). Winter buds separated into two freshweight groups, i.e., one averaging 0.047 g and the other 0.264 g, showed progressively poorer survival, lower biomass, and fewer rosettes in turbidities ranging from less than 1 to 45 NTU (about 53 to 7 percent incident light). Survival of small winter buds was about 50 percent at low turbidities (≤ 15 NTU), and was very poor (0 to 17 percent) under the most turbid conditions. Large winter buds survived well (> 85 percent) at turbidities up to 15 NTU, but in the highest turbidity treatment, survival was lower and more variable (50 to 83 percent). New winter bud production was greater in plants grown from the large winter buds, and trends in winter bud number in response to turbidity mimicked those of plant biomass production.

Table 6 Vegetative establishment of <i>V. americana</i> in relation to abiotic (a) and biotic (b) factors		
Factor/Type*	Establishment	Reference
Dissolved Inorganic Carbon (a)	CO ₂ enrichment stimulates carbon uptake rates, and can potentially offset growth limitation due to infertile sediment and low pH	Titus & Stone 1982, Barko et al. 1991a, Titus et al. 1990, Titus 1992, Titus & Andorfer 1996
Herbivory (b)	Establishment may be protected through use of exclosures to protect against grazing by waterfowl, turtles, muskrats, manatees, and carp	Carter & Rybicki 1985, Hauxwell et al. 2004, Smart et al. 2005
Light (a)	Young plants from winter buds can elongate in the dark	Korschgen & Green 1988
	Over a range from 2 to 25 percent full sun, plants from winter buds can produce new replacement-weight winter buds in 9 percent light or more; extending the growing period enables winter bud formation at a lower light (i.e., 5 percent full sun) level	Kimber et al. 1995b
	Low levels of light diminish vegetative growth and biomass production	Barko et al. 1991a
Salinity (a)	Tolerates to between 5 and 10 ‰ when other conditions are suitable (e.g., light)	French & Moore 2003
	May tolerate salinity as high as 12 ‰ or more if increase or fluctuation in salinity is gradual	Twilley & Barko 1990, Doering et al. 2001
	Duration of exposure to high salinity is important in determining plant survival and ability to recover when conditions become suitable	Doering et al. 2001
Sediment (a)	Grows well on fine-textured, inorganic sediment with organic matter content < 20 percent; sands potentially low in nutrients; high organic content diminishes sediment stability, and increases organic acid concentrations to levels that may be toxic for growth	Smart & Barko 1985
Temperature (a)	Growth diminished at cold temperatures of 16 °C or less; 28 to 32 °C optimal for growth; high temperature, somewhere between 30 and 35 °C can greatly diminish new winter bud production	Barko et al. 1982, 1984; McFarland & Barko, unpubl. data
Turbidity (a)	Winter buds showed progressively poorer survival and fewer rosettes over a range from <1 to 45 NTU; large winter buds survived and grew better than small winter buds at all experimental turbidity levels	Doyle & Smart 2001
Water Movement (a)	Waves generating a shear velocity of about 1.4 m s ⁻¹ can reduce biomass, plant height and new rosette development	Doyle & Smart 2001
	Within a range of slow currents for which flow is laminar (0.02 to 0.5 cm s ⁻¹) photosynthesis increases with increases in velocity	Westlake 1967
Winter Bud Size (b)	Mortality increases with decreases in winter bud size (e.g., weight, length)	Titus & Hoover 1991, Doyle & Smart 2001

Although *V. americana* has a relatively high thermal optimum, it potentially can grow over a wide range of water temperatures. According to Barko et al. (1982, 1984), plants from winter buds were greatly diminished in dry biomass, shoot density, and length at water temperatures of 16 °C or less (Table 6). Growth increased with increases in temperature from 16 to 28 °C, with thermal optima achieved mainly at 28 to 32 °C. Patterns of response to differences in temperature were magnified at moderate to high levels of light, confirming significant interactive relationships between these two factors. Presently, information is generally lacking on growth at temperatures > 32 °C but detrimental effects on winter bud formation between 30 and 35 °C have been detected in *V. americana* (McFarland and Barko, unpubl. data) and other SAV species (McFarland and Barko 1999). Low numbers and biomass of these propagules resulting from high temperature exposure can lead to low population densities and smaller plants at the start of the next growing season.

Water currents and waves are key environmental factors affecting SAV establishment, distribution, and morphology, particularly in shallow waters. In some cases where movement is slow, water current serves as an important auxiliary energy source by increasing the availability of plant nutrients and exporting waste products (Davis and Brinson 1980). Within a range of slow currents for which flow is laminar (0.02 to 0.5 cm s⁻¹), Westlake (1967) demonstrated that photosynthesis of SAV in the laboratory increased with increasing current velocity. On the other hand, reductions in size or complete absence of SAV in very shallow areas may be due in large part to water abrasion (Hutchinson 1975, Davis and Brinson 1980). Doyle and Smart (2001) demonstrated that waves 0.15 m high generating about a 1.4-m s⁻¹ shear velocity can impede the growth and reproduction of *V. americana* from winter buds (Table 6). In their study, wave-treated plants produced significantly less biomass, had shorter leaves, and fewer new rosettes than did untreated, control plants. They concluded that *V. americana* subjected to wave activity might spread less rapidly and be less resilient in facing other environmental stresses (e.g., herbivory, poor water quality, water level fluctuation). Their findings concur with those of flume investigations showing that damage to aquatic plants, including *V. americana*, increases with wave heights above 0.1 m (Stewart et al. 1997). Kimber and Barko (1994) have reviewed direct and indirect effects of water movements on aquatic plant communities and should be consulted for further information on these issues.

V. americana is considered a freshwater plant that can grow at low salinities but is usually limited between 5 and 10 ‰ (Bourn 1932, 1934; Haller et al. 1974; Davis and Brinson 1976; Staver 1986; Doering et al. 2002; French and Moore 2003). It has been noted in oligohaline regions of the Pamlico and Caloosahatchee River estuaries and is a dominant component of SAV in the transition zone of the tidal Potomac River (Davis and Brinson 1976, Carter and Rybicki 1985, Kramer et al. 1999). Early studies showed that growth from winter buds, identified as *V. spiralis*, peaked at 2.8 ‰ and remained high at 4.2 ‰, but ceased at 8.4 ‰ and greater (Bourn 1932, 1934). Haller et al. (1974) found that over a range from 0.17 to 16.65 ‰, young transplants grew best at 0.17 to 3.33 ‰, failed to grow at 6.66 ‰, and died and decayed at 13.32 ‰. Occasionally, the plant is found at relatively high salinities (~ 10 to 15‰) in the field, but in many cases, the exposure varies in strength, occurs gradually, or is short-lived due to tidal influences (e.g., Davis and Brinson 1976, Doering et al. 2002). Laboratory studies (Twilley and Barko 1990, Doering et al. 2001) have demonstrated *V. americana* may survive at salinities of 12 ‰ or more if the increase in salinity is gradual or of short duration. Close examination of the methodologies of studies under controlled conditions allude to the importance of the length and strength of the exposure, and plant age in determining salinity tolerance limit.

V. americana is seldom found growing at a pH < 6 (Crow and Hellquist 1982; Korschgen and Green 1988, Table 6) and thus appears vulnerable to effects of lake acidification. Grisé et al. (1986) reported that young transplants accumulated 76 percent less biomass and produced fewer rosettes and fewer winter buds at pH 5 than at pH 7.5. Later studies by Titus and Hoover (1993) showed that reproductive output was markedly reduced, both sexually and asexually, in plants grown from winter buds and seeds at low pH (Table 3). Their results on winter bud production generated the “closing spiral” hypothesis that exposure to low pH can eventually extinguish the population. Low pH can trigger a decline by reducing plant growth and reproduction through progressively smaller numbers and sizes of individual winter buds. This hypothesis was supported by field transplant investigations where *V. americana* growth measured as plant number and size quickly declined in two acidic lakes in the Adirondack Mountains (Titus and

Hoover 1993). The results were in direct contrast to those from an alkaline lake where *V. americana* transplants grew vigorously and accrued far greater biomass than in the above acidic lakes (Overath et al. 1991).

Present evidence suggests that rooted species of SAV derive the bulk of their mineral nutrition from nutrient pools, especially N and P in sediment. Because of the greater demand and more rapid uptake of N by SAV, P appears less important than N in regulating SAV growth in many instances. For example, sediments from the Upper Mississippi River that were fertilized to increase available N promoted an approximate 30- to 50-percent increase in aboveground production of *V. americana* from winter buds (Rogers et al. 1995). In contrast, P additions to the same sediment had little overall positive effect on growth, consistent with findings of previous in situ fertilization experiments (Anderson and Kalff 1986, Duarte and Kalff 1988, Moeller et al. 1988). Barko et al. (1991b) proposed that SAV may be more frequently limited by N than by P due to relatively larger pools of P in most lake sediments.

Establishment of SAV can be greatly affected by sediment through textural impacts on rooting success and nutrient impacts on biomass (Sculthorpe 1967). Typically, *V. americana* grows well on fine-textured inorganic sediments with organic matter content less than 20 percent (cf. Smart and Barko 1985, Barko et al. 1986, McFarland, pers. obs.). Smart and Barko (1985) reported that, on fine-textured mineral sediments, SAV yields frequently exceed 1200 g dry wt m⁻² sediment surface area. Sediments that are high in sand content tend to be nutritionally poor substrates for growth and may impede rooting success due to resistance to root penetration (Barko et al. 1991b). Low levels of organic matter in such sediments can promote vegetative growth by enhancing ionic exchange and increasing nutrient concentrations (Sand-Jensen and Søndergaard 1979, Kiøboe 1980). Conversely, high organic matter content may be detrimental to growth because of toxic concentrations of organic acids and low density of the sediment (Ponnamperuma 1972, Barko et al. 1991b).

Dissolved inorganic carbon (DIC) has been cited as a possible factor limiting rates of photosynthesis and growth of aquatic vegetation (Sculthorpe 1967, Barko et al. 1986). The photosynthetic potential of a variety of SAV species appears to far exceed photosynthesis determined by carbon available in many aquatic systems (Browse et al. 1979, Beer and Wetzel 1981). Increases in DIC have been demonstrated to stimulate carbon uptake rates (e.g., Steeman-Nielsen 1947, Titus and Stone 1982, Wetzel et al. 1985) and help overcome growth limitation of *V. americana* on infertile sediment (Barko et al. 1991a; Titus 1992, Table 6) and at low pH (Titus et al. 1990). Titus and Andorfer (1996) noted dramatic increases in dry biomass of *V. americana* on both high and low fertility sediments, with CO₂ amended to 10 x ambient (i.e., 130 µM). Moreover, with CO₂ enrichment, the increase in dry biomass on both sediments was greater at pH 5 than at a near neutral pH (7.3).

In nature, *V. americana* is subject to control by a variety of grazers including muskrats, red-bellied turtles, manatees, carp, and especially waterfowl. In 1980, waterfowl consumed 40 percent of 380,160 kg (dry weight) of *V. americana* winter buds on a portion of Pool 7 of the Upper Mississippi River (Korschgen et al. 1988). In a matter of days, grazing by manatees decimated newly transplanted stands of *V. americana* left unprotected in Kings Bay, in Citrus County, Florida (Hauxwell et al. 2004). Grass carp introduced into Lake Wingra in the late 1800s apparently caused *V. americana* to disappear from the lake by 1929 (Davis and Brinson 1980).

One year after carp removal by rotenone in the Middle Harbor of Lake Erie, Ohio, *V. americana* was found where it had not been found before treatment.

A few studies of herbivory on *V. americana* have employed full exclosures or fenced plots that offer some degree of protection (Table 6). Carter and Rybicki (1985) studied transplanted *V. americana* in the Potomac River and observed that plants grown in full exclosures during their first year became well-established in the field the following year. Recently, Sponberg and Lodge (2005) reported that exclosures to limit waterfowl foraging provided refuge for aquatic plants, especially *V. americana*, subject to intense seasonal grazing. Moreover, in an extensive manual to guide the establishment of aquatic plants in the field, Smart et al. (2005) recommended different types of exclosures and planting strategies beneficial to establishing *V. americana* and other aquatic vegetation. While exclosures can be advantageous, they may require intense upkeep and monitoring (e.g., in tidal areas) to prevent clogging that may lead to light limitation and other detrimental impacts on the plants.

FUTURE RESEARCH NEEDS: This review presents evidence of two ecotypes of *V. americana* whose life histories reveal important differences in modes of over-winter survival. While the northern ecotype produces winter buds as its sole means of perennation, the southern ecotype may die down in winter to a reduced evergreen condition. Data thus far suggest that the southern ecotype does not produce winter buds and that its lack of winter bud formation may be an inherent characteristic. Morphological differences may also exist between these two ecotypes—differences that may account for the two variants, i.e., narrow-leaved and broad-leaved, observed by Lowden (1982). Though his descriptions did not address differences in winter bud formation between variants, it is interesting that the illustrations in his article were based on specimens from Ohio and Texas, respectively. Further research is needed to clarify differences between ecotypes of *V. americana* to determine ability to survive in different localities and risks of hybridization to population fitness.

The length of time a seed remains viable is critical to population longevity, since the potential for growth exists as long as a single seed remains germinable in the substrate. Gradients in the sedimentary environments where seeds become lodged, as well as the internal (genetic and physiological) properties of seeds may be important to understanding processes that may delay or speed seed germination. Further knowledge of what controls the timing and quality of germination would be useful to:

- Predict depletion and replenishment rates of the seed/propagule bank
- Develop protocols for planting and habitat restoration
- Understand relationships between seed viability and depth of burial
- Anticipate the size and viability of the seed bank from one year to the next

Establishing the influences of salinity on the growth and survival of *V. americana* is central to understanding its distribution and abundance in tidally influenced estuaries. While much work has been conducted on growth from winter buds and transplants of this species, little is known about the effects on establishment of seedlings. Further research is needed to determine tolerance limits of seedlings to salinity, particularly considering duration and strength of exposure, and seedling age or stage of development.

Thus far, flower induction in *V. americana* has received little investigative attention but should be examined in relation to different factors (especially photoperiod, light, spectral quality) to determine critical levels. In addition, the positive relationship between incidence of flowering and plant biomass, as determined in the laboratory (cf. Titus and Hoover 1991), warrants further investigation under field conditions.

Propagule dispersal is a critical feature governing SAV distribution, but little is known regarding controlling factors in the dissemination of *V. americana*. For SAV in general, three principal disseminating agents are recognized, including: water, animals (including man), and wind, but they differ greatly in relative importance. Wind dispersal is believed to be hazardous and rare for SAV, since propagules are likely to be transported to terrestrial or other areas where development would be restricted. Water dispersal is also likely to cause high propagule mortality, although it may provide an important means of establishing in new areas. Both external and internal transport by animals, especially waterfowl, have been reported but it is now recognized that many animals, including man, can potentially disperse SAV propagules. With specific regard to the dispersal of propagules of *V. americana*, it would be of interest to assess:

- The relative roles of different modes of transport and deposition
- The importance of sexual versus asexual propagules in establishing new populations
- Survival of seed and other propagules after passing through digestive tracts of waterfowl and other known grazers

Ecological studies of SAV propagules should consider handling of propagules in a manner that does not compromise collected data. It is essential that pre-study conditions be maintained as near as possible to conditions found in nature and do not interfere with experimental treatments that are being tested. Special attention should be given to:

- Removal of propagules from substrate (changes in light and redox)
- Method and duration of storage (changes in temperature and moisture)
- Sterilization and scarification (modification of the seed surface)
- Use of Petri dishes without a substrate

Baskin and Baskin (1998) have provided guidelines to help reduce experimenter bias in seed studies, and many of their proposals could apply to the handling of vegetative propagules.

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